

BURROWING BEHAVIOR OF THE SEA ANEMONE *PHYLLACTIS*

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There are a number of sea anemones from different families of actinarians that are known to burrow into sand or mud flats. Burrowing is not an aberrant or unique behavior of anemones, but a frequently observed activity. The general characteristics of burrowing have been described by Stephenson (1928), and Ansell and Trneman (1968) have described the fluid dynamics of burrowing in the sea anemone, *Peachia hastata* Gosse. The following study was undertaken in order to explain burrowing behavior in terms of the neuromuscular organization of the anemone, *Phyllactis concinnata*, and to compare burrowing with other well known anemone activities (Batham and Pantin, 1950b, 1954; Ross and Sutton, 1967; Pantin, 1952).

MATERIALS AND METHODS

The anemone, *Phyllactis concinnata*, is a member of the family Actinidae found in the Gulf of California and Calloa, Peru (Carlgren, 1949, 1951). The anemones were collected from intertidal sand flats in Cholla Bay, a locality near Puerto Penasco, Sonora, Mexico. They ranged in size from $\frac{1}{2}$ inch to $2\frac{1}{2}$ inches across the oral disc, and from 1 inch to 6 inches in length when the column was expanded. They were maintained in the laboratory in twenty-gallon salt water aquaria with a coarse sand and shell hash substrate.

A Grass S. D. 5 stimulator with insulated platinum electrodes was used to give electric shocks. Stimulus duration was 2 milliseconds, voltage was twice threshold, and stimulus frequency was varied depending on the purpose of the experiment. Three methods were employed to analyze the behavior of these anemones: direct observation, photography of the anemone in various stages of burrowing and the recording of movements with a pen-writer. When recording, three channels of a four channel E and M Physiograph were used to monitor movement while the fourth served as a time base. The motion transducers were isotonic A-myographs to which long lever arms were attached and lightly counter-balanced in order to exert minimum tension on the anemone. One end of a monofilament thread was tied to the end of the lever and the other attached to a thread sewn to the column of the anemone. Extensive anemone muscle movements could be recorded without the digging performance of the anemone being appreciably affected by the slight change in the tension caused by the depression of the myograph spring. The majority of the recordings were made from anemones that had three thread loop attachments sewn to the sphincter muscles. The attachments were made at equal distances around the column as determined by counting the mesentary insertions. After an anemone had been attached to the

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levers, it was placed in a one-gallon aquarium filled with sea water with a two-inch layer of sand on the bottom. The water was aerated continuously and temperature was maintained between 20.5° and 22° C. In most experiments the physiograph records were accompanied by direct observations over long periods of time in order to attribute the appropriate activity to recorded movements. Certainly the effect of tying anemones to levers cannot be discounted, but observations in the laboratory and in the field indicate that such behavior as digging is little changed by attachments.

RESULTS

Gross morphology

Carlgren (1951) has given a description of *Phyllactis concinnata* found in the Gulf of California. Gross dissections and examinations of histological sections during this study confirm his findings and emphasize the following points. The column is smooth except for 40 to 48 longitudinal rows of verrucae at the top. These are small adhesive vesicles which adhere to bits of shell and sand grains. Above the verrucae lies a ruff or collar which may be as much as 4 inches in diameter. The ruff is characteristic of the genus and is formed of fronds which bear a variable number of papillae. It is very sensitive to tactile stimuli and may also serve a chemosensory function. The oral disc is small, and surrounded by 40 to 48 tentacles. The pedal disc is well developed, an unusual feature in a burrowing anemone. Internally, there are usually two siphonoglyphs and 20 to 24 pairs of perfect mesenteries. The strong longitudinal retractors are located on the endocoelic surface of all mesenteries except the directives. On the opposite side of each mesentery there is a thin sheet of transverse radial fibers. Growing over these in the bottom half of the column are well developed parieto-basilar muscles. There are strong parietals, which run longitudinally on each side of the mesenterial attachment of the column, and form a continuous band with the parieto-basilar in the upper part of the column. Circular muscles line the column and oral and pedal discs. There is a weak sphincter muscle below the ruff.

Compared to the musculature of non-burrowing forms, that found in the burrowing anemones differs in development rather than in kind of muscles. The burrowing anemones have very powerful retractor muscles to execute a quick withdrawal (Batham and Pantin, 1950a). The sphincter muscle of these anemones is not well developed, and the only method by which one can produce a sphincter closure is by excessive electrical stimulation. The sphincter muscle takes part in the fast closure reflex of both *Metridium* and *Calliactis* (Robson, 1961). The *Phyllactis* does not exhibit this protective closure of the oral disc. As in *Stomphia* (Sund, 1958), the parieto-basilar muscles of *Phyllactis* are well developed and serve an important function in the attachment and movement of the pedal disc.

Histology of the nervous system

Some success was attained in staining the nervous system of *Phallactis* with methylene blue following Pantin's (1952) method. There is a comparatively dense network of large bipolar cells on the surface of the retractor muscle. The length of these cells was determined by observing the freshly stained preparations

with an ocular micrometer, and the maximum length seen was 6 mm in the fully relaxed muscle. In preparations where the muscles were not fully relaxed, the cells appeared to be as long as in a relaxed one, but their course on the surface above the folds of the muscle was not as direct and they were more difficult to measure. The nerve net is sparse on the radial surface of the mesentery. No multipolar cells are found on the mesentery, and the column has few bipolar cells and no multipolar cells. Sense cells are small but numerous, particularly at the junctions of the mesenteries and the column, in the oral disc, and in the tentacles. The nerve net of *Phyllactis* does not appear to be basically different from that of *Metridium* or *Calliactis*.

Responses to electrical stimuli

The *Phyllactis* exhibits the characteristic facilitated response that has been described for other anemones (Pantin, 1935; Pantin and Vianna Dias, 1952). There is normally no response to a single shock applied to any part of the column or ruff. However, with repetitive stimulation there is a symmetrical shortening of the column to each shock after the first if the interval between stimuli is shorter than 1.5 seconds at 21° C. As in other anemones, this response is considered to be brought about primarily by the contraction of the retractor muscles.

In *Phyllactis* the facilitating effect of the stimulus is influenced by the temperature. At 10° C the longest interval between the first stimulus and a second which will produce 5% of the maximum response is 3 seconds, at 21° C the interval is 1.5 seconds, and at 32° C it is less than a second. These values are within the range of those recorded for *Metridium* and *Bunodactis* (Pantin and Vianna Dias, 1952). As is true for *Bunodactis* there is no obvious adaptation of the facilitation rate of *Phyllactis* to the tropical temperature range.

Parietal contractions have been studied quite extensively in *Metridium* (Batham and Pantin, 1950b), *Calliactis* (Needler and Ross, 1958), and *Bunodactis* (Pantin and Vianna Dias, 1952). These contractions of the column are slow and have a variable latent period. *Phyllactis* also exhibits these typical slow responses when shocks are given at too low a frequency to elicit a retractor response. Another response that occurs frequently is elicited by several stimuli at a low frequency or by a single shock applied to the side of the column. Then there is a sharp bending of the column usually towards the stimulating electrodes and it would appear that bending is due to a contraction of the parieto-basilar muscles. A similar response to a single stimulus is seen in *Stomphia* and is thought to be a contraction of the parieto-basilar muscle (Hoyle, 1960).

Analysis of the burrowing behavior

The buried anemone. *Phyllactis* buried in the sand flats of Cholla Bay has only the ruff, oral disc and tentacles exposed. When the tide is out the ruff and oral disc may be covered with sand, or withdrawn into the burrow. When the tide starts to come in, the anemones elongate until the oral disc is level with the top of the burrow again. Strong mechanical stimuli will cause the anemone to withdraw. In the laboratory greatest activity can be evoked when live brine shrimp are added to aquaria, at which time the tentacles are extended and wave about.

Apart from these feeding movements and periodic elongations and withdrawals, anemones are not very active in a burrow. Physiograph records confirm this and show that buried anemones exhibit arrhythmic activity.

The burrowing anemone. A *Phyllactis* placed on any of a variety of sand substrates starts digging in a few minutes. Burrowing is initiated when the anemone is in a contracted state and upright on the substrate. Muscle contractions associated with digging are rhythmical, and a number of muscle systems are intimately involved. In brief, digging appears to be accomplished by a shortening of the column which acts as a hydrostatic skeleton and forces fluid into the inflated pedal disc and the disc into the sand. This is followed by an elongation of the column as the animal prepares for the next contraction. The anemone continues to dig until it reaches hard substratum, either a rock or large shell fragments. The amount of time required for an anemone to dig in completely varies with the anemone, the temperature and the substrate, but under ordinary environmental conditions it takes less than 2 hours. The rhythmic contractions cease once the anemone is attached to the substratum.

The various phases of burrowing behavior are diagrammed in Figure 1. A shortening of the column (Fig. 1A) may be regarded as the first step in burrowing. Typically such a movement is said to be due to parietal activity (Pantin, 1952; Batham and Pantin, 1954). However, if the pedal disc is hooked up to one myograph and the mid-column and the sphincter to the other two, the physiograph record shows that the first contraction in the pedal disc occurs approximately 30

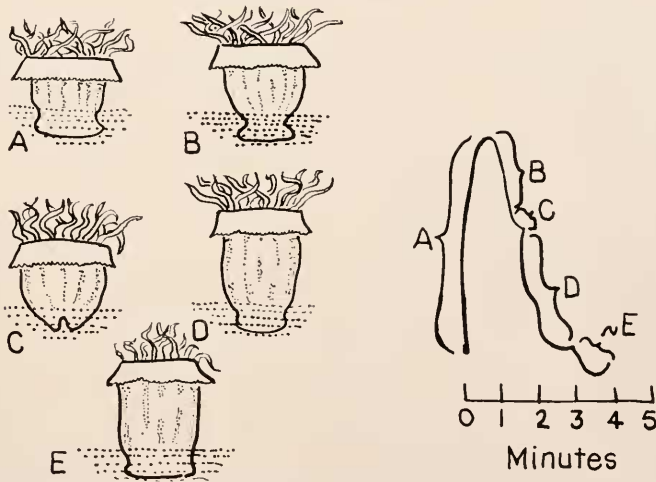


FIGURE 1. On the left is the diagrammatic representation of the various phases of burrowing behavior in the sea anemone, *Phyllactis concinnata*. "A" is the shortening of the column, which is followed by a circular muscle contraction passing down the column as shown in "B," and in "C" the pedal disc constricts. Then the pedal disc begins to enlarge and the column lengthens in "D" and "E." On the right is a physiograph tracing representing a single contraction as recorded from one of three attachments to the column. The brackets "A" through "E" show how the tracing is correlated with the burrowing phases shown on the left. As the column contracts, there is an upward movement of the pen as seen in "A," and the column elongates and the pen moves downward as seen in "B" through "E."

seconds before any in the column or ruff. This would seem to indicate that the parietal-basilar muscles contract in unison first and this action is followed by a simultaneous contraction of all parietals. There must also be a slow contraction of the retractors for the oral disc to pull down symmetrically (Batham and Pantin, 1954).

Following column shortening, there is elongation as the parietals and parietal-basilar relax and a peristaltic wave of circular muscle contraction moves toward the pedal disc (Fig. 1B). The circular muscle contraction appears as a band or as a wave of increased tone moving down the column and, as has been noted (Batham and Pantin, 1951), it effectively causes the elongation of the column. When the circular muscle contraction reaches the pedal disc, which is quite inflated during the parietal contractions, the latter constricts and assumes a concave shape (Fig. 1C). However, within 30 seconds to a minute the pedal disc begins to enlarge again and to assume a convex shape as water flows in and the parieto-basilar and circular muscles relax (Fig. 1D). This latter movement detaches the pedal disc from any rock or shell to which it may have adhered during the contraction of the parietals. Once the pedal disc is fully inflated, the parieto-basilar contractions reoccur, followed by the parietal contractions. Some records show an occasional quick contraction of the retractor muscle during digging. This is a random event which occurs after the animal has started digging. Such a contraction forces water out of the column through the anemone's mouth and makes the anemone smaller. The smaller anemone then settles into a larger hole. A quick contraction often occurs upon the cessation of the rhythmic digging movements as well.

It appears that the integrity of the hydrostatic skeleton must be maintained. If the column is damaged or cut in any way, the anemone will not dig in, and will eventually die. Cuts in the pedal disc do not prevent burrowing, presumably because holes can be sealed by muscular contraction, whereas weak muscles of the column are ineffective in preventing fluid loss.

Physiograph records of a digging anemone show the time course and extent of movement during each phase of the digging period. Phase "A," (Fig. 1) represents the shortening of the whole column as the parieto-basilar muscles and the parietals contract simultaneously. The subsequent change in slope marked "B," represents the relaxation of the parietals and the elongation of the column due to the peristaltic wave. There is a plateau at "C," sometimes with a slight peak. This represents the time when the anemone settles into the substrate as the peristaltic wave reaches the pedal disc and the latter deflates. "D" represents further elongation of the column as there is an increase in tone in the circular muscle and the pedal disc fills with water. This is the stage preceding the next parietal contraction. In some recordings there is a fifth phase, "E" which represents a final elongation occurring immediately before contraction.

The rhythmic quality of the contractions is shown in Figure 2. There is a simultaneous contraction of all parietal muscles during digging. Physiograph records of the digging movement of different anemones are quite similar, not only in pattern, but in time course. In more than 30 records from anemones collected at different times of the year, the most frequently measured interval between the parietal contractions was 4 minutes at 21°C. The interval between contractions

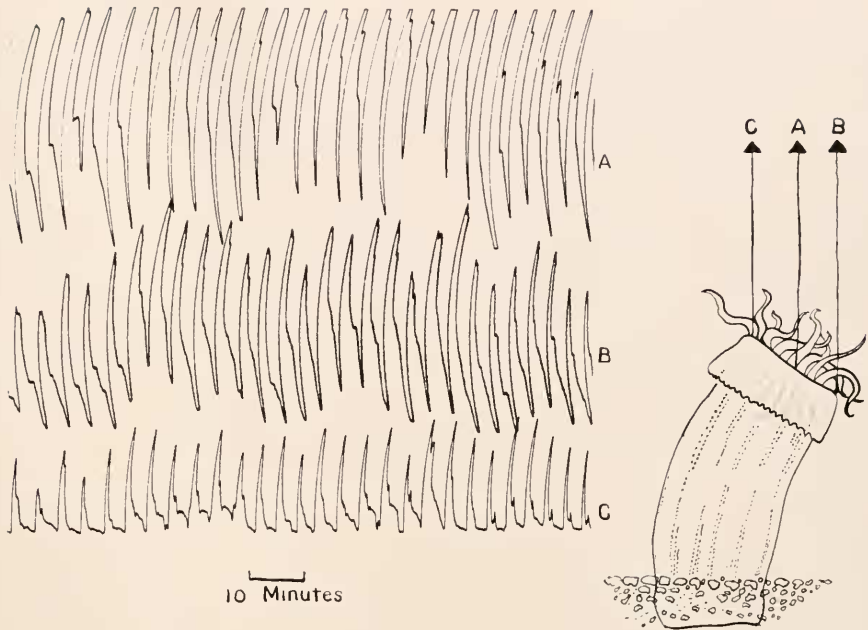


FIGURE 2. A portion of an actual physiograph record from a burrowing *Phyllactis* with three attachments on the column. Each contraction of the column caused all three pens to move upward simultaneously. In this instance the anemone was at a slight angle, and tracings "A" and "B" show more amplitude because of this. This portion of the record is nearly 2 hours long and the consistency of the rhythmic contractions is clearly seen.

may be somewhat longer or shorter at the beginning or the end of the digging activity, however.

Burrowing in *Peachia hastata* Gosse (Ansell and Trueman, 1968) is a similar process, but this anemone has a physa instead of a pedal disc. When the anemone is burrowing the physa undergoes a cyclical change of shape as "introversion and then eversion" occurs. This change of shape is due to the peristaltic contraction of the circular muscles, which is followed by contraction of the longitudinal musculature and which results in fluid being forced into the physa. According to Ansell and Trueman, the physa serves as a "physal anchor" during the column contraction. Also, the physa starts the initial penetration at the onset of burrowing, as the anemone lies on the substrate. After about $\frac{1}{3}$ of the anemone has penetrated the sand, the cyclical change of shape of the physa is accompanied by sharp contractions of the column musculature. These contractions do not occur with each introversion and eversion cycle, and the interval between the contractions increases as the burrowing progresses. This is in contrast with the *Phyllactis* where a major contraction of the column occurs with each inflation of the pedal disc.

Specimens of *Phyllactis* were observed after they were released in their natural habitat. Anemones placed in a small tidepool began to dig within 10 minutes. By the time an hour had passed they were quite well dug into the substrate. As far as could be determined the burrowing movements of these animals in the natural habitat were the same as those of the anemones in the laboratory. On the other hand, specimens of *Phyllactis* released in open waters were rolled about on the sand and were unable to burrow.

The effect of food on the burrowing behavior. Five of fifteen specimens of *Phyllactis* buried in an aquarium were taken out of the sand and then placed back on the surface. None of the fifteen had been fed for a week. Once the five started digging actively some brine shrimp were released into the water. Only the buried anemones showed feeding activities, and they would catch as many as 10 shrimp each before they stopped feeding. On the other hand, brine shrimp that swam into the tentacles of digging anemones would not be caught and held. These experiments suggest that there is a change in threshold for nematocyst discharge during digging, or an inhibition of the entire feeding process. A similar response is reported by Ross and Sutton (1964) for *Stomphia*.

The effects of mechanical and electrical stimuli on a digging anemone. Anemones pulled out of the sand after they start burrowing will resume digging if placed on the sand, or will continue contracting rhythmically if placed on a hard substratum such as a glass plate. In the latter instance the rhythmic contractions become part of a pedal locomotion, allowing the anemone to move off of the plate and dig back into the sand. Mechanical stimuli of different strengths applied with a glass rod elicit responses ranging from the slight twitch of a tentacle to complete withdrawal (retractor response) of an anemone that is in a burrow. Light touches do not effect the overall behavior of a digging anemone. On the other hand, a strong stimulus will evoke a retractor response during any phase of the digging. However, digging anemones recover from this stimulus quickly and continue their rhythmic activity.

On no occasion did electrical stimuli of any sort elicit rhythmic digging behavior in an inactive anemone lying on the surface of the sand. Electrical stimuli did have some effect on burrowing animals, however. A series of stimuli were given to digging animals during various phases of the digging activity at a frequency and voltage that would elicit either a parietal or a retractor response in a non-burrowing animal. The results show that often a parietal response will occur during the contraction or relaxation phase of burrowing if shocks are given at a low frequency, and the rhythmic pattern of digging is not upset. A retractor response is produced by shocks of sufficient frequency during any phase of the burrowing, and if the retractor response occurs during the column contraction it does not alter digging behavior. However, a retractor response during the "C" or relaxation phase seems to increase the extent of the relaxation before the next contraction.

DISCUSSION

The burrowing behavior is another example of the way in which the sea anemones carry out a coordinated activity. The rhythmic contractions of the longitudinal and circular muscles of the column manipulate the fluids of the

column's hydrostatic skeleton so that the pedal disc is pushed into the substrate. One of the most interesting features of this behavior is the very rhythmic sustained contractions of the column. In studies of more than 30 anemones of different sizes, the 4-minute interval between contractions was remarkably consistent, and rhythmic contractions could be maintained for as long as 6 hours. Burrowing behavior is probably under the regulation of a system which controls the timing and sequence of each muscle contraction. There is evidence that the control system not only initiates burrowing and acts positively to keep it going, but that it inhibits other activities, such as feeding behavior, as well. There are two possibilities for such a control system. One would be that each contraction of the column could be dependent on the excitation set up by the preceding, as in a chain reflex; the other would be that the control system involved a pacemaker.

It appears that the control system does involve a pacemaker. This is the best explanation for the consistent interval between contractions in the different anemones. If the contractions were under the control of a chain reflex, it would seem that the interval would vary from one anemone to another. Since the spread of the excitation is slow, there would be a longer interval between contractions in an anemone with a column measuring 6 inches than in one with a column that measures 1 inch, but this is not true. The continuation of the rhythmic contractions when the anemone is pulled out of one substrate (sand) and put on another (glass) is best explained by a pacemaker system. Furthermore, the contraction interval is not affected by a variety of substrates. If the burrowing were controlled by a chain of reflexes, and if one substrate could be penetrated more readily than another, each step in the behavior could be completed sooner and the interval between the contractions would be shortened; this is not the case. The rhythmicity of burrowing behavior is not unique to *Phyllactis*. Ansell and Trueman (1968) report that a burrowing *Peachia hastata* Gosse has rhythmic contractions of the column musculature with intervals of usually $1\frac{1}{2}$ minutes. It is difficult to pinpoint the location of the assumed pacemaker or pacemakers in the *Phyllactis*. Multipolar cells that are suggested as a pacemaker system for *Stomphia* (Robson, 1963) are not obvious in the column.

Pantin (1952) described a number of different functions for the column "action system" of anemones, including maintenance of shape, movement in feeding and locomotion. Burrowing is another adaptation of the column action system. A control system with its pacemaker element in a burrowing anemone could be similar to one that permits other anemones to undertake pedal locomotion. My own studies (unpublished) of another species of *Phyllactis* and *Bunodosoma cavernata* show that column contractions of these anemones are rhythmic as they move laterally along the surface and this is remarkably similar to pedal locomotion in *Metridium* (Batham and Pantin, 1950c), and *Stomphia* (Ross and Sutton, 1967). Pantin (1965) suggested that rhythms as in the normal parietal-circular muscle contractions of *Metridium* may have origins from local pacemakers. Slight modifications of this basic capacity for rhythmic coordinated activity has permitted anemones to develop a varied behavior. Further study of the nature and origin of this basic rhythmicity could be made by taking advantage of the predictable, consistent and sustained nature of the rhythmicity found in the burrowing behavior of anemones.

It is not known if these anemones, when in their natural environment, move out of the sand and then burrow again. *Phyllactis* in the laboratory aquaria will stay in one location for years, as long as they are undisturbed and the water is well filtered and aerated. In their natural environment *Phyllactis* might be washed out of their burrow by a severe storm. The fact that burrowing activities can be initiated quickly would be of adaptive advantage when this occurs. Digging is not triggered by a specific stimulus as is the swimming behavior of *Stomphia* (Robson, 1961), but is activated by a set of conditions such as the locomotor phase of *Metridium* (Batham and Pantin, 1950c). There are fewer conditions for digging than for locomotion however, in fact, only three. The pedal disc must be unattached, there must not be any sand around the column, and there must be a soft substrate available. Cessation of burrowing occurs when the column is completely buried and the pedal disc is attached to a firm substrate. Other marine invertebrates burrow by pushing a rhythmically contracting foot or proboscis into the sand (Trueman, 1967). It is interesting that anemones accomplish the same thing albeit at a slower rate, but with a much less complex organization of neuro-muscular tissue.

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SUMMARY

1. The burrowing behavior of the anemone *Phyllactis* is a very consistent and predictable activity.
2. Burrowing is accomplished by rhythmic contractions of the column musculature around a hydrostatic skeleton, with the result that fluid is alternately forced into and withdrawn from an inflatable pedal disc. This rhythmic activity forces the disc into the sand.
3. The interval between contractions is approximately 4 minutes at 21° C. A pacemaker or set of pacemakers is postulated.
4. Under unusual conditions rhythmic movements may continue for hours. Normally, however, the anemone stops digging within 2 hours. After the pedal disc reaches a hard substratum and sand surrounds the column rhythmic activity ceases.

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